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# Nomenclature of parthenogenetic, gynogenetic and "hybridogenetic" vertebrate taxons: new proposals*



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**In order to homogenize, standardize and simplify the nomenclature of parthenogenetic, gynogenetic and "hybridogenetic" vertebrate taxons, new proposals are made, which rely on a clear separation between the need of a single nomenclatural system at the species level for all living animals, and that of a distinction between different kinds of evolutionary units in nature.**

**Three major kinds of species-rank taxons can be distinguished in animals: (1) species (s. str.), or bisexual species, with sexual reproduction (including normal meiosis, usually with recombination, fertilization of egg by sperm, and non-clonal inheritance); (2) kleptons, which depend on sexual parasitism for their reproduction, and which include zygokleptons (with sexual reproduction, "hybridogenetic" meiosis, fertilization of egg by sperm, and hemiclonal inheritance) and gynokleptons (with parasexual reproduction, modified meiosis or ameiosis, gynogenesis, and clonal inheritance); (3) klonons, with parasexual or asexual reproduction, modified meiosis or ameiosis or absence of gametes, parthenogenesis or absence of germ, and clonal inheritance. All these evolutionary systematics categories are considered here to be of the same nomenclatural rank within the Linnaean system, that of species, and names of the corresponding taxons should be submitted to the same rules, those of the *International Code for Zoological Nomenclature* for species names. To distinguish kleptons and klonons from species (s. str.), it is suggested to add the abbreviations "kl." and "kn.", respectively, between the generic and the specific names.**

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## Introduction

Many papers have recently been devoted to the study of several vertebrate "forms" of hybrid origin and that display particular modes of reproduction and of inheritance, such as parthenogenesis, gynogenesis, and "hybridogenesis". The "forms" studied belong to the bony fishes (*Poecilia* and *Poeciliopsis*: see e.g. Schultz, 1977, Monaco, Rasch & Balsano, 1984, Moore, 1984 and Vrijenhoek, 1984; *Phoxinus*: see Dawley, Schultz & Goddard, 1987), the urodeles (*Ambystoma*: see e.g. Bogart, 1982, Bogart & Licht, 1986 and Bogart et al., 1985, 1987), the anurans (*Rana*: see e.g. Dubois, 1977 and Graf & Polls Pelaz, 1989) and the saurians (*Lacerta* and *Cnemidophorus*: see e.g. Cole, 1975, Uzzell & Darevsky, 1975 and Dessauer & Cole, 1986; *Lepidodactylus*: see e.g. Ineich, 1988).

Some, at least, of these "forms" have genetic and evolutionary particularities which distinguish them from "normal species", and several authors have found it necessary to formally recognize these particularities by giving them special "names" or even by ascribing them to new taxinomic[1] categories. The proposals in this respect are diverse, including refusal of any particular nomenclature (Maslin, 1968; Uzzell, 1982; Frost & Wright, 1988), the use of letters or numbers (Schultz, 1961, 1966, 1967; Zweifel, 1965; Cole, 1985; Walker, 1986; Ineich, 1988), the use of compound Latin names (Schultz, 1969, 1977; Cook & Gorham, 1979; Génermont, 1980; Lowcock, Licht & Bogart, 1987), the use of normal simple Latin names between quotation marks (Hubbs & Hubbs, 1932; Günther, 1973; Günther & Hähnel, 1976; Dubois, 1977, 1979; Koref-Santibañez, 1979; Bogart, 1980) and the use of normal simple Latin names preceded by a special mark or sign (Dubois & Günther, 1982).

This diversity of approaches is understandable in the first period of a research, but I feel that we have now reached the time where some standardization is necessary. The proposals made in the present paper are a new contribution towards this aim, which comes after a few other ones and benefits from the comments of various authors (Maslin, 1968; Lazell, 1971; Cook & Gorham, 1979; Mishler & Donoghue, 1982; Cole, 1985; Walker, 1986; Lowcock, Licht & Bogart, 1987; Frost & Wright, 1988; Echelle, 1990 a-b; Frost & Hillis, 1990) on this controversial question.

## Some desirable properties of taxinomic systems

Why should we *name* things? I do not think that it is in order to express their "essence", but rather in order to be able to *communicate* about them, to carry some *information* about these things, and in this respect the best nomenclatural system will be the one having the highest generality and universality.

1. I use the correct spellings "taxinomy" and "taxinomic" instead of "taxonomy" and "taxonomic", following Pasteur (1976) and Fischer & Rey (1983).

Systematics is the discipline of biology which has the purpose of *classifying* living beings, that is of ascribing them to *taxons*[2], and of *naming* them.

Systematics is not, or should not be, an intellectual game, or a simple search for intellectual elegance. All biologists need a *taxinomic system* (that is, a classificatory and nomenclatural system) to be able to *communicate* about the living beings they study, and to carry some *information* about these things.

To be theoretically satisfactory and acceptable by all biologists, any taxinomic system should have some properties, among which the following ones can be stressed: unicity, universality, univocality, homogeneity and stability.

(1) *Unicity*: there should be a single taxinomic hierarchy for all living beings, not several.

(2) *Universality*: the taxinomic system should be devised in such a way as to be able to accomodate *all* living beings ever to be found in the real world, not only some of them. This means that taxinomic concepts must bear some determined relationship to *universally observable patterns and particularities* of the organisms of the real world (or of the natural processes involved in the evolution of these organisms), rather than being derived solely from some general *theory*, such as a theory of evolutionary process, or a theory of biological classification.

(3) *Univocality*: the classificatory and nomenclatural system should be univocal, that is, any given living being should unambiguously be ascribed to a given and single place in the system.

(4) *Homogeneity*: there should be some equivalence, by some criteria, between various taxons ascribed to the same category within the taxinomic hierarchy.

(5) *Stability*: the taxinomic system should display at least rather important stability, so that every new discovery should not be liable to modify it partly or totally. This stability should concern both the classificatory pattern and the nomenclature.

## THE LINNAEAN SYSTEM

Many different classificatory and nomenclatural systems have been proposed since the beginnings of biology. The only one to have survived for more than two centuries and which, despite various criticisms, is still very healthy, is the Linnaean system of taxinomic hierarchy (a hierarchy of categories) and of Latin binominal nomenclature. Despite its unavoidable limitations, this system has shown until now a great flexibility and has been used with success by biologists having widely divergent ideas of what biological classification should be. Until a better system is ever proposed and shown to be better, any

2. Terms such as "taxon", "phenon", "klepton" or "phylum" are not true ancient Greek or Latin names but modern terms which only bear a formal resemblance to old Greek or Latin names. They should therefore be given normal plurals like "taxons" or "phylums", not artificial ancient Greek or Latin plurals like "taxa" or "phyla". This suggestion follows the advice given in this respect by *The Oxford Guide to the English Language* (ANONYMOUS, 1984: 27): "It is recommended that the regular plural (in *-s*) should be used" [for such words], "even though some are found with either type of plural". Furthermore, for a sake of homogeneity, the term *phylon* should be preferred to "phylum".

taxinomic discussion and proposal should clearly place itself within the frame of the Linnaean system of taxinomic hierarchy and of Latin binominal nomenclature, such as it is recognized and formalized by the International Codes of Nomenclature. This implies in particular that *taxons should have names*, Latin names following the International Rules, and on the reverse that such names should *not* be given to entities which do not qualify as taxons.

On the other hand, acceptance of the Linnaean system does not imply any particular choice as to the philosophy of classification to be used, be it the empiricist, the pheneticist, the cladistic or the evolutionary one. These philosophical choices only have consequences in what concerns classification, but not, at least not directly, nomenclature.

## Taxon, phenon, genon, phylon

When we deal with taxinomy, we deal with the recognition, delimitation, ordering and naming of *taxons*, or taxinomic units. The question must therefore be asked: what is a taxon? According to Mayr (1969: 4), a taxon is a group of organisms which is considered by taxinomists as "sufficiently distinct to be worthy of being assigned to a definite [taxinomic] category". This definition is rather vague and does not help us very much to distinguish taxons from other types of "groups of organisms". But, as a matter of fact, if we ask for more precise definitions, systematists will give us different ones according to the "school" of taxinomy in which they belong. In this respect, it will be useful to examine briefly a few different kinds of "groups of organisms" which may be recognized by systematists.

One such kind is the *phenon*. Mayr (1969) has used this term for a phenotypically reasonably homogeneous sample at the species level. The term *morphospecies* has also been used by some authors for the same category. In a strictly phenetic approach to systematics, the terms taxon and phenon would be equivalent. On the other hand, systematists who take it for granted that a meaningful and "natural" classification of living beings is possible only if based on the study of the phylogenetic and evolutionary relationships between them, that is, cladists and evolutionary systematists, reject the strict correspondence between taxon and phenon, and point to many cases where this correspondence does not hold at all. Several different phenons may be part of a single taxon (the simplest example being that of the males and females of the same species), while on the reverse several different taxons may belong to the same phenon (for example, different dualspecies or sibling species; see Bernardi, 1980).

Another kind of units which is not often recognized by systematists, but which is of particular relevance to the problems being discussed here, consists of those units which can be recognized on the sole basis of structural genetic similarity. For such genetic units, the new term *genon* would appear convenient. Similarity of genotypes is most unlikely to be a result of convergence between different lineages, and therefore usually a genon is also a taxon. However, in all cases where hybridization is involved, similar genotypes can occur repeatedly through independent hybridization events, and in such cases a genon may not correspond to a single taxon — at least for cladists and evolutionary taxinomists, who consider that different lineages should be referred to different taxons. Examples of genons which would not, for them, correspond to taxons, would be interspecific hybrids between two species obtained independently by several hybridization events, or, more narrowly, groups of parasexual or asexual individuals shown to have identical electrophoretic markers at some loci, but without evidence (for example from skin grafting experiments) that they originated from the same founder event.

Other kinds of units may be recognized by biologists. I will mention only two examples: (1) "ecotypes" or "ecospecies", characterized by their ecological niches or adaptive zones; and (2) *phylons*, that is, complete lineages or historical entities. The latter are considered by cladists as strictly equivalent to taxons, while for evolutionary systematists taxons are also based on lineages but do not automatically correspond to complete phylons or lineages (whenever genetic, phenetic and ecological divergence has occurred during the history of a phylon, the latter may correspond to several taxons).

## NOMENCLATURE OF PARTHENOGENETIC, GYNOGENETIC AND "HYBRIDOGENETIC" TAXONS

Let me now approach the specific problem of the nomenclatural treatment of parthenogenetic, gynogenetic and "hybridogenetic" vertebrate taxons on the basis of these general statements.

First of all, it must be stressed that the problem is: how should we name some particular *taxons*? This excludes from this discussion particular *organisms* which do not qualify as *taxons*. Thus, "hybrids as such", that is, organisms which arose as the individual results of phenomena of hybridization between species or between hybrids, but which do not give rise to particular lineages separated from those of their parental species, do not qualify as parts of independent entities or taxons. They should therefore not be given taxons names, that is Latin binominals written in italics and composed of a generic name and of a specific name, even if these are presented as "informal names". Therefore, for example, instead of *Ambystoma laterale-jeffersonianum*, the corresponding animals should be designated as simple hybrids, as follows: *Ambystoma laterale* × *jeffersonianum*. If "informal systems" are proposed for the designation of individual organisms, these systems should be devised in order to avoid any possible confusion between taxons and non-taxons: therefore they should be based for example on letters or numbers rather than on Latin binominals.

Secondly, for those entities which qualify as taxons, general rules of nomenclature must be devised. These rules must be compatible with the Linnaean system of taxinomic hierarchy and Latin binominal nomenclature, in order to maintain the unicity, universality and homogeneity of this system. They must make sure that *all* the peculiar taxons in question be included in the system, even those which appear rather "atypical" as compared with the "traditional" species concept.

One must avoid confusing two different problems. On one hand, for philosophical reasons of unicity, universality and homogeneity, the nomenclatural system cannot consist of several different, independent and parallel, hierarchies: that is, a simple hierarchy is required, and, in the Linnaean binominal system, any organism should at least be referable to one taxon of rank genus and to one taxon of rank species. This means that any living organism should be liable to be given a specific name (or two or several, linked by crosses, in the exceptional cases of "hybrids as such"). On the other hand, these philosophical constraints on nomenclature do not bear at all on our understanding of biological phenomena as they occur in nature. There is no philosophical or biological reason why all organisms in nature should belong in similar biological historical entities governed by similar laws: it is perfectly understandable and acceptable that some organisms belong to bisexual species, while others belong to asexual or parasexual taxons. The only constraint which our adherence to the Linnaean system implies is that these asexual or parasexual taxons should in nomenclature be given the rank of species. Homogeneity in the nomenclatural treatment of taxons of the same rank does not imply that these taxons are biologically identical or homogeneous.

Bisexual species and asexual or parasexual "pseudospecies" (as DOBZHANSKY, 1970, called them) all usually belong to well-defined genera. The nomenclature of any of these species-rank taxons consists therefore of a generic name followed by a specific name. The latter should in all cases conform with the rules of the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985), including all the rules about conditions of availability of names, use of type-specimens, priority and homonymy, etc. In many cases, asexual or parasexual taxons of the species rank have been recognized, described and named long before their biological particularities were discovered, and in all these cases, they should retain the names first given to them. In other cases, these taxons should be named by the same procedures as "normal" species.

However, since different types of species-group taxons of the species rank may be recognized in the living world, differing in particular in their modes of reproduction and of inheritance, it appears useful and justified to indicate some of these differences by writing the names of these taxons in a special way. In this respect, several suggestions have been made for the nomenclature of asexually or parasexually reproducing forms, especially among vertebrates of hybrid origins. Some of these suggestions, for example the use of letters such as A, B or C, or of symbols such as Cx, Cy or Cz, may be rejected immediately, as non-Linnaean. Other ones include the placement of the species-group name of these taxons between quotation marks, and the use of compound names indicating the basic genotype of these forms. I discussed elsewhere with Rainer GÜNTHER the reasons for rejecting these proposals, and we proposed another system (DUBOIS & GÜNTHER, 1982). We suggested that names of "atypical" species-rank taxons such as kleptons should be simple, not compound, Latin names, but that attention should be drawn to the particularities of these taxons by placing a special symbol between the generic name and the specific name of such taxons. Thus for example, in the case of kleptons, the abbreviation "kl.": *Rana* kl. *esculenta*.

## THREE DIFFERENT KINDS OF SPECIES-RANK TAXONS

How many different types of species-rank taxons can we recognize in animals? I suggest that, despite the vast diversity of local and particular situations, all cases can be referred to three major categories, one of which itself includes two rather distinct subcategories. However, before presenting these categories in more detail, I wish to make two preliminary comments.

The first comment concerns the use of the term *hybridogenesis*. This use is extremely confusing for several reasons. First of all, this term has been used for a very long time in the biological literature to designate the simple phenomenon of appearance of a hybrid through hybridization of two organisms belonging to two different taxons. On the other hand, SCHULTZ (1969) proposed to use the same term to designate a particular type of reproduction, which occurs in some *Poeciliopsis* of hybrid origin. This second meaning is completely different from the original one. For this reason, BORKIN & DAREVSKY (1980) proposed the replacement name *creditogenesis* for the concept called hybridogenesis by SCHULTZ (1969).

But, besides this homonymy problem, both SCHULTZ's hybridogenesis and BORKIN & DAREVSKY's creditogenesis are confusing for a second reason: they are defined as "a reproductive mechanism", and most authors tend to view them as concepts similar to those of gynogenesis or parthenogenesis, which bear similar names. But the latter concepts designate particular modes of *starting the development of an egg*, and they do not imply by themselves any particular kind of meiosis: while gynogenetic or parthenogenetic taxons do indeed have particular kinds of meioses, which give rise to particular types of eggs, parthenogenesis or gynogenesis can also occur sometimes spontaneously, or can be artificially induced, in normal bisexual species and in normal eggs. On the other hand, hybridogenetic reproduction involves only a particular kind of gametogenesis, while the starting of egg's development follows a normal pattern (with fertilization). For this reason, I think it useful to dissociate the concept of "reproductive mechanism" into two distinct concepts: (1) mode of formation of gametes, or *gametogenesis*; and (2) mode of starting of egg's development, for which I propose the general term of *germinogenesis* (from the Latin *germen*, which gave "germ", the term by which embryologists call the active egg starting its development, divisions, etc.). Usually germinogenesis occurs by fertilization, which gives rise to a zygote, and can also be called *zygogenesis*. Other kinds of germinogenesis are *gynogenesis* (the sperm stimulating the egg to develop without true fertilization) and *parthenogenesis* (development of a virgin egg, which can be started by various factors).

In what follows, I am provisionally retaining the term hybridogenesis, since it is now well established, but in a restricted sense: rather than a "mode of reproduction", it means here a particular type of gametogenesis which, whatever its cytological mechanisms may be (actually there apparently exist several of them, and even rather distinct ones), results in the exclusion of one complete (or almost complete) parental chromosome set and in the formation of a gamete having a pure (or almost pure) chromosomal complement from the other parental species.

Now to the second comment. What should be the criterions for deciding that a particular asexual or parasexual form, with clonal or hemiclonal inheritance, is a taxon of species rank? These criterions will depend on the philosophical school of biological classification chosen. For systematists of the phenetic school, overall phenetic and genetic similarity will be the major criteria. For systematists of the cladist school, any lineage resulting from a given founder event will be afforded taxinomic recognition, and lineages resulting from distinct founder events will be considered distinct taxons. Finally, for evolutionary systematists, the latter condition also applies, but on the other hand when a major phenetic, genetic and/or ecological shift has occurred within a single lineage as a result of mutation, it may be warranted to recognize distinct taxons within this lineage.

Now I shall present briefly the three major types of species-rank taxons which I suggest to distinguish in animals, and which I had already pointed out briefly in a previous paper (Dubois & Günther, 1982: 294-295). Despite the vast array of particular cases observed in nature, it seems that the three categories here defined (including one with two rather distinct subcategories) cover all possible cases in existence in the real world.

(1) *Species* (s. str.), or bisexual species.

(2) *Kleptons*, with two subcategories:

(a) "Hybridogenetic" and zygogenetic kleptons, or *zygokleptons*, with zygogenesis and hemiclonal mode of inheritance.

(b) Gynogenetic kleptons, or *gynokleptons* (or *klonokleptons*), with gynogenesis and clonal mode of inheritance.

(3) *Klonons*, that is, all kinds of uniparental "species" with clonal heredity *not* depending on sperm for their reproduction, including, both, species with truly asexual reproduction (for example vegetative reproduction), and species with parasexual or asexual clonal reproduction (for example, autofertilization, thelytoky).

Dubois & Günther (1982) also proposed to recognize as a *synklepton* a group of forms including both one (or several) klepton(s) and the "good species" from which it (they) originated. Similarly, I propose here to call *synklonon* any group of forms including both one (or several) klonon(s) and the "good species" which gave birth to it (them).

If one accepts Dubois & Günther's (1982) proposal to use a sign, intercalated between the names of generic and specific rank, to recognize these special species-rank taxons, different signs should be used for the different types of taxons, in order to avoid any possible confusion. Dubois & Günther (1982) proposed the abbreviations "kl." and "synkl." respectively for klepton and synklepton; these signs, or one of them, were used by a few authors since then (Dubois, 1982, 1983, 1984; Günther, 1983, 1987; Günther & Koref-Santibañez, 1983; Burny & Parent, 1985; Monnerot, Dubois & Tunner, 1986; Ohler, 1987, 1989; Polls Pelaz, 1987, 1988; Berger & Günther, 1988; Günther & Plötner, 1988; Plötner, Günther & Schade, 1988; Crespo, Oliveira & Paillette, 1989; Graf & Polls Pelaz, 1989; Polls Pelaz & Graf, 1989). I here propose the abbreviations "kn." and "synkn." respectively for klonon and synklonon.

The principal characteristics of interest to systematists of the types of taxons defined above are shown in Table 1. Both species (s. str.) and klonons are reproductively independent, while both zygokleptons and gynokleptons depend on sexual parasitism for their reproduction (and for their survival) and are therefore not reproductively independent. Both gynokleptons and klonons display a clonal mode of inheritance, while zygokleptons have a hemiclonal one.

Table I. – The principal genetic and reproductive characteristics of the different evolutionary taxinomic categories of species rank: species (s. str.), klepton (zygoklepton and gynoklepton) and klonon.

| Name and symbol | Species (s. str.) | Klepton (kl.) Zygoklepton (zykl.) | Klepton (kl.) Gynoklepton (gykl.) | Klonon (kn.) |
|---|---|---|---|---|
| Examples | | *Poeciliopsis, Rana* | *Poeciliopsis* | *Cnemidophorus, Lacerta* |
| Sexes | Both | ♀ or both | ♀ | ♀ |
| Free intrabreeding | Yes | No | No | No |
| Reproduction | Sexual | Sexual | Parasexual | Parasexual or asexual |
| Gametogenesis | Normal meiosis (usually with recombination) | "Hybridogenesis": modified meiosis or ameiosis | Modified meiosis or ameiosis | Modified meiosis or ameiosis or absence of gametes |
| Germinogenesis | Zygogenesis (fertilization) | Zygogenesis (fertilization) | Gynogenesis (pseudo-fertilization) | Parthenogenesis or absence of germ |
| Sperm necessary | Yes | Yes | Yes | No |
| Sexual parasitism | No | Yes | Yes | No |
| Reproductive independence | Yes | No | No | Yes |
| Mode of inheritance | Not clonal (recombination between parental genomes) | Hemiclonal (clonal inheritance of one parental genome) | Clonal | Clonal |

## Final questions

Two remaining problems are worth discussing before concluding

(1) Should gynogenetic forms be included in the category klepton or in the category klonon? A purely formal genealogical approach to taxinomy would lead to include them in the category klonon, since they have the same clonal mode of inheritance as parthenogenetic forms. For those who would favor such an approach, the categories and subcategories listed above and shown in Table I could be arranged differently, as follows: (1) *species*; (2) *zygokleptons* (or *kleptons* s. str.); (3) *klonons*, with two subcategories, (a) *gynoklonons* (or *kleptoklonons*), equivalent to *gynokleptons* in Table I, and (b) *parthenoklonons*, equivalent to *klonons* in Table I.

But, as an evolutionary systematist, I think that the fact that gynogenetic forms depend on the sperm of another species and are therefore not reproductively independent is very important and should be stressed by placing them in the category klepton: their dependence on the sperm of another species implies for these forms the inability to escape from the geographical range of that species, and the extinction of the latter also results in their own extinction. True parthenogenetic forms are very different from them in not having these limitations.

Furthermore, gynogenetic forms use sperm for their reproduction, and there is always some danger in using sperm: even if you don't want to, you run the risk of being fertilized, and this is indeed what occurs for example in some *Phoxinus* gynokleptons or in some *Ambystoma*.

Finally, it should be stressed that the same synklepton can include both zygokleptons and gynokleptons (see for example the *Poeciliopsis occidentalis* synklepton), which stresses the fact these two kinds of taxons are closely related and that the passage from one to the other one is easy.

(2) Should zygokleptons be considered taxons of the species-rank or of a lower rank? This question may be asked if we consider for example WILEY's (1978) definition of the evolutionary species as "a lineage of ancestral descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendancies and historical fate". Strictly speaking, zygokleptons are not true lineages but half-lineages[3], and for their "second half" they do not maintain identity from the lineage which provides the genetic material, nor do they have their fully independent evolutionary tendancies and historical fate, since their history is directly related to the history of the species on which they depend for their perpetuation. I can see three possible solutions to this problem.

One would consist in considering a klepton as formally being part of the ancestral bisexual species which provided the part of its genome which is clonally transmitted in the klepton. Another one would consist in considering it as formally being part of the bisexual species which allows its perpetuation (and which is also usually, but not always, one of the ancestral species from which it arose by hybridization). In both these symmetrical cases, the klepton category would be a category of subspecific, and not specific, rank, and names of kleptons would be written in the following way: *Rana lessonae* kl. *esculenta*.

The third solution, which I already advocated (DUBOIS & GÜNTHER, 1982), is to consider kleptons as taxons of specific rank, but to indicate the fact that they belong in a wider genetic system by referring them, as well as the bisexual species with which they interact genetically, to more comprehensive taxons, of a rank intermediate between genus and species, and which we proposed to call synkleptons: *Rana* (synkl. *esculenta*) kl. *esculenta*.

This system has the advantage of allowing for the possibility of still recognizing taxa of subspecific rank within kleptons (see MASLIN, 1968 and DUBOIS & GÜNTHER, 1982), which the first one does not allow. Furthermore, it poses no particular problems within the

3. I here disagree with ECHELLE (1990 a-b) who recently suggested that "hybridogens" are full lineages, because "a historical group of hybridogens is connected to an ancestral hybrid individual by haploid genealogical lines (= lineages)" (ECHELLE, 1990 a: 111). This is true, but the same group is also connected to the species with which it has to backcross at each generation: any "hybridogenetic" offspring derives its genome from two parents. It is irrelevant in this respect to point that "in hybridogens, the traits expressed by the species providing the 'borrowed' genome are not entrained in the germ line" [of the "hybridogen"] (ECHELLE, 1990 a: 111). These traits are also transmitted by a germ line, that of the "parasitized" species. We should not forget that we are classifying living *organisms*, not germ lines, or, put in other words, that the object of taxinomy is the *soma*, not the *germen*.

frame of Linnaean nomenclature, while the first one poses problems when the kleptic name happens to be nomenclaturally older than the specific one (this is the case in the example used above: *lessonae* Camerano, 1882 would have priority over *esculenta* Linné, 1758). For these reasons, I here maintain my support to the nomenclatural system first proposed by DUBOIS & GÜNTHER (1982).

## CONCLUSION

The recognition of the three distinct evolutionary taxinomic categories of species (s. str.), klonon and klepton (the latter with the two subcategories of zygoklepton and gynoklepton), three categories considered here to be of the same nomenclatural rank (that of species), should clarify discussions on the problems of nomenclature of taxons belonging to the second and third of these categories. The proposals made here, in particular that of adding a sign (kn or kl.) between the generic and specific name, are currently not acceptable within the rules of the *Code* now in force (ANONYMOUS, 1985). Such rules are however liable to be modified, if zoologists feel that the proposals made above are useful, and apply to the International Commission on Zoological Nomenclature for such a modification. The rules have already been changed many times to incorporate new proposals, for example, recently, concerning the nomenclature of some infrageneric and supraspecific taxons (see e.g. BERNARDI, 1980), and could well be modified as well in this case.

## RÉSUMÉ

De manière à homogénéiser, standardiser et simplifier la nomenclature des taxons parthénogénétiques, gynogénétiques et "hybridogénétiques" de Vertébrés, de nouvelles propositions sont faites, qui s'appuient sur une séparation nette entre le besoin d'un système nomenclatural unique pour tous les animaux au niveau spécifique, d'une part, et celui d'une distinction entre différents types d'unités évolutives existant dans la nature, d'autre part.

Trois types principaux de taxons de rang spécifique peuvent être distingués chez les animaux: (1) les espèces (s. str.) ou espèces bisexuées, à reproduction sexuée (comportant une méïose normale, avec habituellement recombinaison génétique, fécondation de l'oeuf par un spermatozoïde et hérédité non-clonale); (2) les kleptons, qui dépendent d'un parasitisme sexuel pour leur reproduction, et qui comportent d'une part les zygokleptons (à reproduction sexuée, avec méïose "hybridogénétique", fécondation de l'oeuf par un spermatozoïde et hérédité hémiclonale) et d'autre part les gynokleptons (à reproduction parasexuée, avec méïose modifiée ou absente, gynogenèse et hérédité clonale), (3) les klonons, à reproduction parasexuée ou asexuée, avec méiose modifiée ou absente ou gamètes absentes, parthénogenèse ou absence de germe, et hérédité clonale. Toutes ces catégories de systématique évolutive sont ici considérées comme étant du même rang nomenclatural au sein du système linnéen, le rang spécifique, et les noms des taxons correspondants devraient être soumis aux mêmes règles, celles du *Code International de Nomenclature Zoologique* pour les noms spécifiques. Pour distinguer les kleptons et les

klonons des espèces (s. str.), il est suggéré d'ajouter les abréviations "kl." et "kn.", respectivement, entre les noms générique et spécifique.

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